

Stubby-winged Mutants of *Limenitis* (Nymphalidae) — Their Occurrence in Relation to Photoperiod and Population Size

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Abstract. Stubby-winged mutants occurring in *L. archippus* and in two forms of *L. arthemis* are reported and described. The genetic control of this character differs in the two closely related species, involving a single autosomal locus in a Maryland strain of *L. archippus*, and two separate loci in an inbred Vermont strain of *L. arthemis*. Phenotypic expression of this trait may be related to external factors such as larval exposure to long diel photoperiod or to pathogens and local reductions in population size.

Introduction

The occurrence of shortened or "stubby-winged" mutants among Lepidoptera has been reported previously among five economically important moths (Robinson, 1971). These include the pyralids *Anagasta kuehniella* (Zeller) and *Galleria mellonella* (L.), the lasiocampid, *Lasiocampa quercus* L., the selidosemid *Cocallis elinguaris* L., and the bombycid, *Bombyx mori* L. Such mutants possess rounded wings, the base to apex distance being considerably fore-shortened. Often this condition is apparent in the pupal wing-disks prior to adult emergence. In both *Anagasta* and *Bombyx* several genes are involved in the expression of this trait. I know of no similar reports of this condition among butterflies. Totally "wingless" forms, however, have been reported in two pierids: *Pieris napi* L. (Bowden, 1963) and *Tatochila sterodice* Stgr. (Shapiro, 1983).

The purpose of this paper is to report shortened or stubby-winged mutants encountered while collecting, breeding and rearing eastern North American *Limenitis* (*Basilarchia*) butterflies. I have recently reviewed the evolutionary relationships of the nearctic species of this genus (Platt, 1983). Stubby-winged mutants have been found in the Viceroy, *L. archippus* (Cramer) from Maryland, the banded purple, *L. arthemis arthemis* (Drury) from Vermont, and the red-spotted purple, *L. arthemis astyanax* (Fabricius) from Maryland. The nature of stubby wings in each of these butterflies will be described.

L. ARCHIPPUS (Cramer)

From January through June 1976, I reared a number of broods of *L. archippus* and *L. arthemis-astyanax* at the University of Liverpool in England. These strains were established by rearing third instar (half-grown) diapausing larvae from hibernacula collected along small streams on the U.M.B.C. campus in Catonsville, Baltimore County, Maryland. *Limenitis* larvae enter facultative diapause during the late summer and fall months in response to short daylength and overwinter in hibernacula constructed from silk-covered tubular bases of willow leaves. The numbers and kinds of hibernacula collected, and adults reared from them are given in Table 1. Larvae were induced to emerge from the hibernacula on two separate occasions, and were reared subsequently on fresh leaves of weeping willow (*Salix babylonica* L.) from the nearby Ness Gardens. Detailed methods for overwintering hibernacula, diapause termination and rearing the larvae have been published previously (Clark & Platt, 1969; Kean & Platt, 1973; Frankos & Platt, 1976).

Table 1. Hibernacula collected in Catonsville, Maryland and adults reared from them in Liverpool, England, during April-May 1976.

Larval Group	Date Collected	Foodplant	No. & Percent Hibernacula with Larvae		No., Kinds & Percentages of Adults Reared	
			Live	Dead	<i>L. archippus</i>	<i>L. astyanax</i>
I. (n=34)	23 XII 75	<i>Salix fragilis</i>	25 (74%)	9 (26%)	8 (4mm, 4ff)	2mm (40%)
II. (n=14)	13 I 76	<i>S. fragilis</i> & <i>S. dispar</i>	9 (64%)	5 (36%)	7 (4mm, 3ff)	0 (78%)
III. (n=7)	13 I 76	<i>Prunus serotina</i>	6 (86%)	1 (14%)	0	2mm (33%)

Note: Larvae were induced to emerge from hibernacula on 18 March (Groups I and III) and on 9 April, 1976 (Group II). all emerging adults possessed perfectly formed normal-sized wings.

The first rearing experiments were begun in late March. Hibernacula were opened, and those containing live larvae were placed in cups containing fresh willow leaves. Unfortunately, these Group I and III larvae were reared under the ambient photoperiod for Liverpool (53° 29' N. latitude). At this time of year the ambient photophase passes through the critical range for Maryland viceroys going from short-day (12 hr daylength) to long-day (14 hr daylength) between 18 March and 16 April

(Duncombe, 1966). Thus, many of the developing larvae died while molting to the 4th and the 5th instars, as well as during the larval-pupal ecdysis, probably as a consequence of this environmental change (see Clark & Platt, 1969, for a discussion of photosensitivity of *Limenitis* larvae, and Hong & Platt, 1975, for consideration of the photoperiodic threshold dependence upon latitude among different viceroy strains). Only ten Group I adults (40% of the live larvae) and two Group III adults (33%) were reared successfully.

Earlier studies revealed that developing viceroy larvae often die during molting when the photophase to which they are being exposed is abruptly altered (Platt, unpubl. data). This effect probably results from disruption of the normal neurosecretory rhythms involving the controlling hormones (e.g.: ecdysone and juvenile hormone), the proper diel timing and secretory onset of which is important to successful molting in these insects. Beck (1968) believes that photoperiod regulates the temporal organization of the entire physiological system underlying insect development, rather than having direct effects on insect growth itself (see Ingram, 1976). However, the larvae which died in Liverpool did so while molting, and they showed symptoms and behavior like those of larvae that had experienced abrupt photoperiod alterations.

Later, during April 1976 the second set of rearing experiments was begun, using the Group II hibernacula. These larvae were reared under long-day conditions only, and the rearing was more successful (78% of the larvae survived to eclose as adults). All three of the emerging adult females were hand-paired (modified method of Platt, 1969), two of them being bred to the same male. These pairings are comparable to matings which might have occurred in nature (had the hibernacula not been collected), since all of the larvae began their development in the wild. The matings lasted from 1½ to over 4 hours, which is normal for North American *Limenitis*. After pairing, each female was confined separately and allowed to oviposit on *S. babylonica*. Each female lived for nearly three weeks.

Table 2 presents the rearing results from these broods. Stubby-winged mutants were first noted in Brood 1 as the larvae matured and pupated. The wing disks of these pupae were only about two-thirds as long as those of normal ones (Fig. 1), and a large "naked" area on the ventro-lateral region of each was apparent. This naked area was just anterior to the normal abdominal segments, and was covered only by a thin cuticular membrane. Consequently, most of these pupae soon collapsed and dried up. Butterflies developed in several others, but then died before emerging.

Just four mutant butterflies eclosed (Fig. 2). These insects expanded their wings as much as possible. Although unable to fly, these stubby-winged butterflies lived for several days, and were able to feed, hop, and crawl around their cages. Two attempts to hand-pair the mutant males to

Table 2. Numbers in F_1 broods of *L. archippus* lab-reared in Liverpool, England during May and June, 1976 on LD photoperiod. Broods 1 and 2 have the same individual male parent.

Brood No.	Eggs	Larvae Hatching	Adults (A) & Pupae (P)		Totals
			Normal	Stubby-winged	
1	242	224 (93%)	86 (A)	31 (P) [2mm, 2ff (A)]	117 (A&P)
2	243	231 (95%)	>100 (A)	0	>100 (A)
3	207	184 (89%)	> 90 (A)	0	>90 (A)

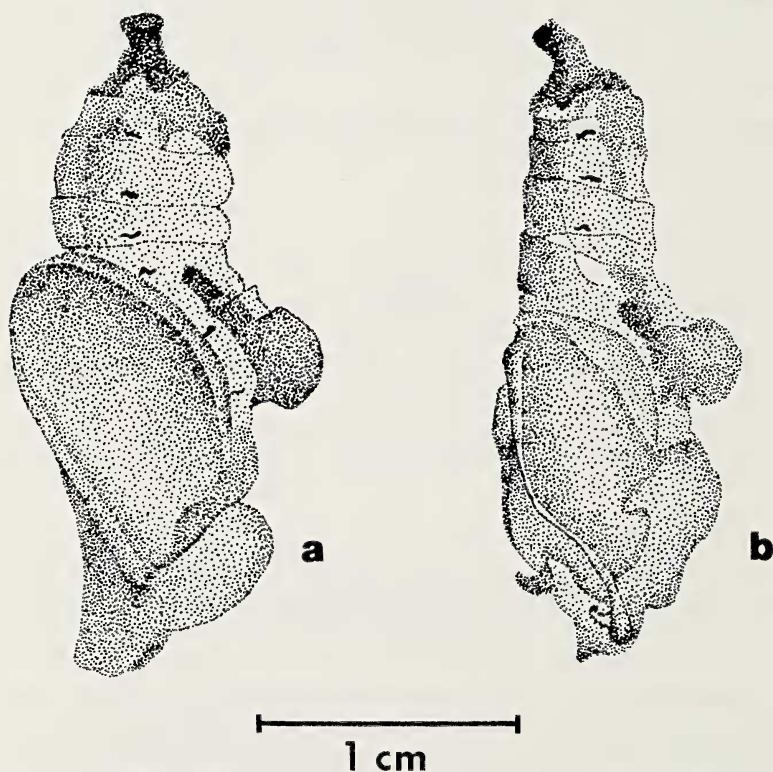


Fig. 1. a) Normal, and b) mutant stubby-winged pupae of *L. archippus* (Cramer) from Brood 1, U.M.B.C. strain reared in Liverpool, England, in 1976 under LD photophase. Drawings from preserved specimens by Jennifer A. Gurany.

normal female sibs failed. Their siblings with normal wings were easily paired, and ten additional crosses were made. These ten females were released in a roof-top greenhouse, where they proceeded to oviposit on potted willows. The females were observed to fly around the greenhouse at random while ovipositing. Each time one landed on a leaf it "drummed" vigorously with its reduced foretarsi. This behavior was immediately followed by uncoiling the proboscis and "tasting" the abraded leaf surface with the sensory tip of the feeding tongue. Only when the leaf was a willow leaf did oviposition follow (see Platt, 1980 for a more detailed discussion of the oviposition sequence). The viceroy strain maintained itself through August, when it died out. Whether or not other mutant pupae arose from these matings is unknown, since I had by then returned to the U.S.

The observed numbers of normal vs. stubby-winged mutants conform to a 3:1 Mendelian ratio [n (normal) = 86, n (stubby) = 31; $EX^2_1 = 0.07$, $p = .78$]. Thus, the stubby-winged condition probably results from a single recessive autosomal gene in *L. archippus*. Both the normal winged wild-collected individuals that had been bred to produce Brood 1 are likely to have been heterozygotes, each carrying a single (unexpressed) recessive gene for this trait. The male of Brood 1 also was the P_1 male of Brood 2, in which no mutants appeared. The Brood 2 female was likely homozygous dominant at this locus.

Field observations of ovipositing female *Limenitis* indicate that *L. archippus* females seek out small willow shrubs or poplar saplings, laying from one to several single eggs per plant, before flying on in search of other plants. The wide dispersal of eggs by each female is an important survival strategy for all species within this genus. Each egg is carefully placed by itself on (or near) a leaf tip, usually on the upper surface (Platt, unpubl. obs.).

Therefore, it seems likely that Brood 1 represents the chance hand-pairing of two sibling individuals, for the following reasons. First, my students and I have heavily collected viceroy and red-spotted purple hibernacula from along the streams, marshy spots, and drainage areas on the U.M.B.C. campus each winter since 1970. Thus, we are familiar with nearly all of the areas where the female butterflies oviposit within the campus environs; these consist mainly of woods-open meadow ecotones in the early and middle stages of old-field succession. Often well over 100 hibernacula are collected from the small scattered willows found in this 476 acre area. Removal of most of the available hibernacula from campus each winter means that the local population must be maintaining itself through the migration of bred females onto the campus from surrounding regions. These consist mainly of deciduous woods and suburban neighborhoods. A few stray colonizing females then could introduce most of the eggs into the newly established annual populations each fall, result-

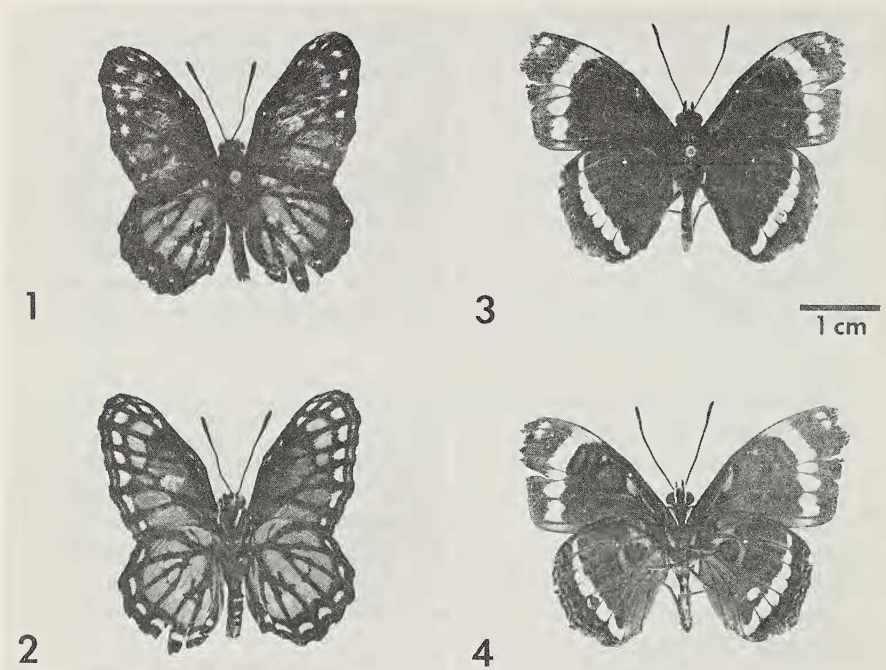


Fig. 2. Stubby-winged mutants of *Limenitis*: 1) and 2) dorsal and ventral aspects of *L. archippus* (Cramer). F₁ male from U.M.B.C. campus strain (Brood 1) reared in Liverpool, England, in 1976; 3) and 4) dorsal and ventral aspects of male *L. arthemis* (Drury), inbred Vermont strain reared in 1977.

ing in Founder effects; 3) Third, the two individuals bred to produce Brood 1 were collected in hibernacula obtained on a single day. Only a total of 14 hibernacula were found in the sublocality searched. Thus, it seems that these larvae well could be the progeny of one or two females which had visited this area during the previous autumn. One of these females possessed the mutant allele in a heterozygous condition, either in her own egg cells, or within the sperm cells she obtained from the male with which she had mated. This being the case, we would expect half of her progeny themselves to be heterozygous for this condition.

If these sibs then were to be inbred at random, one would expect one-fourth of the crosses to be between heterozygous sibs, and three-fourths of them to involve either one or two homozygous (dominant) individuals. The results shown in Table 2 are consistent with these ratios: Brood 1 yielded 25% stubby-winged individuals (in the pupal stage), whereas, broods 2 and 3 produced only normal-winged progeny. The above

Table 3

Occurrence of stubby-winged mutants in six broods of an inbred strain of Vermont Lisenitis arthemis, 1977 data. Chi square analyses I-IV test for maximum likelihood probabilities (ML) for ratios expected if either a single locus or two loci are involved in the expression of stubby-wings.

Brood	Generation	Wing Phenotypes		Totals	Ratios:		I		II		III		IV		Significance
		Normal	Stubby		I (single gene)	II (single gene)	III (two genes)	IV (two genes)							
1) 869	G ₄ (out-cross)	5 (1mm : 4ff)	1m	6	Exp. χ ² P=	(3.0:3.0)	(4.5:1.5)	1:1 2.67 .10	3:1 1.29 .26	(5.25:0.75)	7:1 0.67 .43(ML)	15:1 (5.62:0.37)	1.11 .31	I-IV, N.S.	
2) 874	G ₄ (sib-x)	66 (35mm : 31ff)	7 (4mm : 3ff)	73	Exp. χ ² P=	(36.5:36.5)	(54.75:18.25)	1:1 47.88 < .001	9:25 9.25 < .001	(63.88:9.12)	0.57 .46(ML)	(68.44:4.56)	1.39 .24	I*** II*** III-IV, N.S.	
3) 875	G ₄ (sib-x)	49 (23mm : 26ff)	1m	50	Exp. χ ² P=	(25.0:25.0)	(37.5:12.5)	1:1 46.08 < .001	14.11 1.78 .20	(43.75:6.25)	5.04 -0.24	(46.88:3.12)	1.54 .22(ML)	I-II*** III* IV, N.S.	
4) 877	G ₅ (sib-x)	11 (3mm : 8ff)	1m	12	Exp. χ ² P=	(6.0:6.0)	(9.0:3.0)	1:1 8.33 < .001	1.78 1.78 .20	(10.5:1.5)	0.19 -0.69	(11.25:0.75)	0.09 .76(ML)	I*** II-IV, N.S.	
5) 883	G ₄ (out-cross)	25 (10mm : 15ff)	2mm	27	Exp. χ ² P=	(13.5:13.5)	(20.25:6.75)	1:1 19.59 < .001	4.46 1.78 .036	(23.62:3.38)	0.64 .44	(25.31:1.69)	0.062 .78(ML)	I*** II* III-IV, N.S.	
6) 918	G ₄ (out-cross)	20 (12mm : 8ff)	2mm	22	Exp. χ ² P=	(11.0:11.0)	(16.5:5.5)	1:1 14.73 < .001	2.97 2.97 .08	(19.25:2.75)	0.50 .48	(20.62:1.38)	0.30 -0.61(ML)	I*** II-IV, N.S.	
All Broods		176 (84mm : 92ff)	14 (11mm : 3ff)	190	Exp. χ ² P=	(95.0:95.0)	(142.5:47.5)	1:1 138.13 < .000	31.50 31.50 .000	(166.25:23.75)	4.57 .034	(178.12:11.88)	0.41 -0.53(ML)	I-II*** III* IV, N.S.	

Statistical Analyses (Chi Square)

explanation offers the only logical reasons for why I might have crossed two wild-collected individuals, each bearing the same recessive mutation in a heterozygous state.

LIMENITIS ARTHEMIS ARTHEMIS (Drury)

Other stubby-winged mutants arose in a strain of *L. arthemis* descended from four wild-caught females collected at Starksboro, Addison Co., Vermont, in June and July 1976 (Fig. 2). Eggs were obtained from these females, and their progeny were reared in the laboratory at U.M.B.C. The strain was maintained by inbreeding (sib-pairings) and by out-crossing non-sibs. Six 4th through 6th generation broods yielded a total of 14 stubby-winged individuals (Table 3). These broods were lab-reared on *Salix babylonica* between January and May 1977, at room temperature on a 18L:6D photoperiod. A total of 884 *arthemis* were reared during these experiments which included 31 separate broods. The number ($x \pm s.e.$) of progeny in these broods was 28.5 ± 4.7 individuals, with the corresponding values for each sex being males = 14.9 ± 2.5 , and females = 13.6 ± 2.3 . The sex ratios approach 1:1 in all generations, with most having a slight (non-significant) excess of males. No excessive pupal mortality of the kind encountered in the *L. archippus* strain from Maryland was observed.

The data from each of the six broods as well as the overall totals give maximum likelihood fits to either 7:1 or 15:1 ratios of normal-winged:stubby-winged specimens, respectively, suggesting that these inbred *arthemis* mutants result from two unlinked recessive autosomal loci. The six broods yielding stubby-winged individuals all can be traced back to a single third generation brood which yielded all normal-winged individuals. These normal-winged butterflies presumably included a high proportion of double heterozygotes resulting from prior inbreeding. Once these double heterozygotes are cross-bred the double recessive homozygotes with stubby-wings will appear in subsequent broods. Those individuals having either one or two wild-type alleles at each of the two loci will be of normal wing phenotype, whereas the double recessive homozygotes will be stubby-winged. There is no evidence for sex ratio disturbance among these broods, so that differential lethality does not appear to influence these results. Among these *arthemis* broods the pupal wing pads are fore-shortened, similar to the way they were among the *archippus* mutants described above. These stubby-winged *arthemis*, unlike their *archippus* counterparts, however, were perfectly capable of flying about our lab cages, despite their reduced wing size. Wing reduction in these *arthemis* appears to affect mainly the outer one third of their wings, rather than the entire wings, as in *archippus*.

Assuming random selection of the various parental genotypes during further inbreeding, one would expect to obtain only normal-winged

individuals from 66% of the crosses. Another 25% of the crosses (those involving two double heterozygous parents) would be expected to yield both normal and stubby-winged individuals in 15:1 ratios. Finally, 9% of the crosses (those involving individuals homozygous recessive at one locus, but heterozygous at the other), should throw either 7 normal : 1 stubby, or 3 normal : 1 stubby, depending on how the respective alleles are distributed in the two parents (Table 4).

Maximum likelihood probabilities for the six broods throwing stubby-winged individuals shows that two conform most closely to the 7:1 ratio, whereas, the remaining four fit the 15:1 ratio most closely (Table 3). Close fits to the 3:1 ratio, which result from one of the two loci becoming homozygous recessive in both parents were not observed. The data presented in Table 3 rule out the possibility that a single autosomal locus controls stubby-wings in this *arthemis* strain. Rather, this trait appears to be under the control of two separate autosomal loci. The sex ratios among the six broods yielding stubby-winged individuals all approach 1:1 with the overall sex ratio being 95 males:95 females. However, the sex ratio among the stubby-winged individuals themselves is biased in favor of males (11 males:3 females, $EX_1^2 = 4.57$, $P = .034$). Possibly the phenotypic expression of this trait differs between the two sexes, since the overall sex ratio is undisturbed.

LIMENTIS ARTHEMIS ASTYANAX (Fabricius)

A single male specimen of *astyanax* having matched stubby forewings and normal sized hindwings was hand-netted by P. J. Kean on 27 July 1977 in Anne Arundel Co., Maryland, along Patuxent River Road in Harwood (Fig. 3). Despite its reduced forewings, this specimen was quite capable of flying, and was resting on a tree trunk when it was collected. The forewings of this butterfly are only about one-half the normal length, and their outer margins have a crimped appearance. The symmetry of these fore-shortened wings suggests that their basis is genetic, rather than developmental. Unsuccessful attempts were made to breed this mutant specimen to normal females from our laboratory strains.

DISCUSSION AND CONCLUSIONS

This paper contains the first report of stubby-winged mutants occurring among nymphalid butterflies. A. M. Shapiro (pers. comm.) has had more than one "stubby-winged" gene appear in his colonies of Andean *Tatochila* (Pieridae) which have been maintained at U.C. Davis for the past five years. Earlier he found such mutants in *Colias eurytheme*, and he notes having collected a "semi-stubby" specimen of *L. arthemis* in upper New York State, as well.

It is possible that reduced wing size of this sort may represent a syndrome resulting from pathologic bacterial or viral infections affecting the

Table 4. Frequencies of the various genotypes of normal-winged individuals resulting from crosses involving double heterozygotes, and the probabilities of these genotypes being used in further matings (assuming random selection of the parental genotypes).

Genotypes among Normal-winged Progeny of two Double Heterozygotes	Frequency of Genotypes (among the Normal-Winged Progeny) ¹	Probabilities of the Genotypes being used in Matings between Normal-winged Individuals resulting from A Double Heterozygous Cross ²
1) 1AABB	0.067	0.13
2) 2AaBB	0.133	0.23
3) 1aaBB	0.067	0.10
4) 2AABb	0.133	0.18
5) 1AAbb	0.067	0.02
Subtotals (1-5)	0.467	0.66 (all normal-winged)
6) 4AaBb	0.267	0.25 (15 normal:1 stubby)
7) 2aaBb	0.133	0.07
8) 2Aabb	0.133	0.02
Subtotals (7 & 8)	0.266	0.09 (7 normal:1 stubby or 3 normal:1 stubby)
Grandtotals (Subtotals, plus 6)	1.00	1.00

¹The frequencies among normal-winged individuals are based on proportions of 15 rather than 16 since the stubby-winged individuals (genotypes 1aabb) are phenotypically distinct. All other genotypes are normal-winged, and cannot be told apart.

²These probabilities are the additive totals of crossing each genotype by itself, and by all others. When two separate genotypes are involved the two frequencies are further multiplied by two, since either sex can be represented by each of the two genotypes involved. As one progresses from genotype one through genotype eight only those specific crosses not previously accounted for are included in the row totals.

insect cultures (Shapiro, pers. comm.). This is most likely to occur when high rates of larval mortality are encountered. In the absence of definitive genetic data (e.g., breeding from the "stubby-winged" individuals themselves), this possibility cannot be entirely ruled out. However I consider this possibility an unlikely explanation for the occurrences of stubby-winged *Limenitis*, since no such viral afflictions were noted in my cultures.

A second possibility is that the expression of some or all of these mutants is related to rearing larvae under unusually long photoperiod regimes. Insects in general, and Lepidoptera in particular, are very sensitive to photoperiod, and rely upon this environmental cue to regulate their temporal growth processes in seasonally unstable temperate environments (Pease, 1962; Danielevskii, 1965; Beck, 1968). In odonatan (damselflies and dragonflies) nymphs, both photoperiod and temperature have been shown to influence abnormal wing-pad development (Lutz, 1968, 1974; Ingram, 1976). Thus, the expression of the lab-bred stubby-winged mutants in *L. archippus* and *L. arthemis* may be dependent upon the unusually long photophase to which the developing larvae were exposed. Of course, the proper control experiments have not been done to test this hypothesis.

Nevertheless, it is conceivable that the stubby-winged condition might not have been expressed if these insects had been reared under conditions of ambient photophase for the respective latitudes from which the strains originated. If this were true, then the mutant individuals perhaps represent those which have the greatest photoperiod sensitivity among their strains and broods. I note this possibility because it seems likely that the



Fig. 3. Wild-caught Maryland male specimen of *L. arthemis astyanax* (Fabricius) showing stubby forewings.

butterfly genome is strongly canalized against the expression of such mutants when the insects are grown under ambient environmental conditions (Shapiro, 1981). This is not meant to suggest that these stubby-winged butterflies are merely phenocopies. Normal winged adults were always produced along with them in appropriate genetic ratios.

The three closely related admiral butterflies exhibit similar stubby-winged mutant phenotypes, but the genetic control of this trait appears to differ in *L. archippus* and *L. arthemis*. In the former, stubby wings is controlled by a single recessive gene, whereas, in the latter a pair of loci are involved, with the double recessives only expressing this trait. The control of stubby forewings only in Maryland *astyanax* remains unknown, but probably also has a genetic basis. In *Limenitis*, a number of multifactorial loci affecting wing coloration are known to influence either the forewings or the hindwings (Remington, 1958; Platt & Brower, 1968; Platt, 1975, 1983), and it is likely that a similar mechanism is controlling stubby forewings in *astyanax*.

It is equally possible that the two autosomal loci controlling stubby-wings in *L. arthemis* are acting along the same (or related) developmental pathways as is the *L. archippus* locus. For example, stubby wings in *L. archippus* could be represented by locus *A*, with *a/a* individuals representing the homozygous recessive phenotype. In *L. arthemis* a second locus, *B* could likewise be affecting the stubby-winged phenotype, with doubly homozygous recessive individuals (*a/a*, *b/b*) only expressing the mutant phenotype. If so, then this second locus might have become fixed in the Maryland strain of *L. archippus* studied in Liverpool, and the *A* locus alone produces the effect. Such a theory requires either: 1) that the *B* locus has become fixed for the recessive allele in the Maryland *archippus* strain, or 2) if the dominant *B* allele has become fixed in Maryland *archippus*, then the *a* allele has to have developed differential penetrance in the *archippus* genome, such that it alone (when homozygous) can produce the mutant phenotype.

Finally, it is interesting to note that a few other species of *Limenitis*, as well as a number in the related genera *Ladoga*, *Neptis*, *Pantoporia*, and even a few species of *Adelpha* possess wing size which is only about two-thirds that of *L. populi* and the nearctic *Limenitis*. The stubby-winged mutant genes, thus, may represent an evolutionary reversion toward a smaller ancestral phenotype still present in these other (more primitive) genera.

These results provide evidence that potentially lethal recessive mutant genes are carried in natural Lepidopteran populations, and that such mutations can be expressed among some individuals, especially when founder effects and inbreeding are involved. Such conditions could arise locally when adult populations are small, following physical environmental stresses, habitat destruction, decimation by disease, heavy predation,

parasitism, and/or collecting pressures, any or all of which may contribute to a population bottleneck.

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